DEMOGRAPHY AND REPRODUCTIVE ECOLOGY OF GREAT FRIGATEBIRDS

BY

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ABSTRACT

Frigatebirds (*Fregata* spp.) differ from most Pacific seabirds in fundamental ways, making it difficult to include them in generalizations about seabird management. We present demographic data on great frigatebirds (*F. minor*) on Tern Island, French Frigate Shoals, in 1998-2000. In terms of mating attempts, males were more likely than females to try to obtain a mate but were much less likely to succeed at pairing, and the variation in pairing success was greater for males than females. Although fledging success was high (63.5%), hatching success was below 30% in all three years of this study. Males end their parental care of fledglings sooner than do females, but parental care by both sexes extends into the pair-formation portion of the next breeding season. Plumage data indicate that females do not breed in years following a successful breeding attempt. For males, the findings are less clear; some males may simultaneously feed 1-year-old offspring and tend new nests. In colony-wide counts of frigatebirds, we detected as many as 1,171 males, 1,053 females, and 691 juveniles on the Island at a time. We estimated that in 1999 there were 2,099 males and 1,615 females that nested, out of a pool of approximately 11,195 males that tried to attract a mate and 1,809 females that evaluated potential mates. Because additional birds did not try to breed at all, the total number of adults in the population is larger than this. Using amplified fragment length polymorphism (AFLP) genetic markers, we found no evidence of spatial genetic structure within the Tern Island colony, confirming previous work showing genetic variation between, but not within, breeding colonies.

INTRODUCTION

Biological conservation requires a basic understanding of the life history and demography of focal species (Meffe and Carroll, 1994), and sound management may be especially important—and problematic—for species such as seabirds that are clustered into areas of high density during breeding. Frigatebirds (*Fregata* spp.) are colonially breeding seabirds for which detailed reproductive and demographic data are generally lacking for most parts of their range (Metz and Schreiber, 2002), and generalizing

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from other seabird species may be unwise, given that frigatebirds are extreme among seabirds in their sexual dimorphism (Dearborn et al. 2001a), low wing loading (Metz and Schreiber, 2002), thermal-dependent flight (Weimerskirch et al., 2003), short pair bonds (Nelson, 1975), and long parental effort (Nelson, 1975).

Our previous work with great frigatebirds (*F. minor*) breeding on Tern Island (23° 45' N latitude, 166° 17' W longitude), Hawaii, has shown that these birds are very long-lived (individuals over 40 years of age; Juola et al., in press). They regularly move thousands of kilometers between islands, yet they retain broad-scale genetic differentiation (Dearborn et al., 2003). They typically exhibit a very male-biased sex ratio at the breeding colony (Dearborn et al., 2001a), inbreed slightly when choosing mates (Cohen and Dearborn, 2004), and only rarely exhibit extra-pair paternity (Dearborn et al., 2001a). Finally, reproductive success of frigatebirds on Tern Island is tied to the body condition of the breeding adults (Dearborn, 2001).

Here, we present new data from 1998, 1999, and 2000 to address four basic aspects of reproductive ecology in this Tern Island population of great frigatebirds. First, we compare the pairing success of males and females. Second, we quantify reproductive success at monitored nests. Third, we compare the duration and frequency of breeding of males and females. And finally, we explore the size and structure of the breeding population, based on direct counts, mark-resight data, and spatial analysis of AFLP genetic profiles of breeders.

METHODS

Pairing Success of Males and Females

To assess breeding attempts and pairing success of males and females, we banded and wing-tagged unpaired birds at the start of the 2000 breeding season by capturing them in the breeding colony while they were perched in shrubs at night. Between 23 January 2000 and 30 January 2000, we tagged 79 males, 76 of which were in breeding plumage, and 54 females, 51 of which were in breeding plumage. Subsequently, we surveyed the breeding colony three times per day (at 0900, 1330, and 1700) from 23 January through 15 May 2000 to record the reproductive behavior of these marked individuals. An individual was categorized as attempting to mate if a male's gular pouch was inflated or if a female was performing an inspection of a displaying male, either while making stereotypical low-altitude inspection flights or while perched in contact with a displaying male. For tagged birds that eventually built nests, contents of nests were monitored daily. Based directly on these observations of tagged birds, we calculated the proportion of displaying males that obtained a mate and the proportion of mate-evaluating females that obtained a mate.

Reproductive Success

We measured hatching success in 1998, 1999, and 2000 by making daily or twice-daily checks of individually marked nests from the start of egg laying (typically early February) through early summer (July in 1998 and 1999, May in 2000). In 1999, nests were then followed bi-weekly through December to measure fledging success.

Duration of Breeding Cycle and Breeding Frequency Across Years by Males and Females

During the egg-laying period, from the end of January through May or June, many adults are still feeding 1-year-old offspring from the previous breeding season. Although these 1-year-olds can fly, they still rely on colony visits by their parents for most of their food. We recorded all opportunistic observations of adults feeding 1-year-olds from the first of January to early July in 1998 and late January to early May in 1999 and inferred differences in the duration of parental care from temporal patterns in the proportion of feedings made by males versus females. During these feeding observations, we also recorded plumage coloration of the provisioning adult. Comparing their plumage to that of birds currently incubating eggs or brooding new chicks allows an assessment of whether the pool of adults caring for 1-year-olds is different from the pool of adults with new nesting attempts. We assessed the plumage of all males that were incubating eggs or brooding young chicks on Tern Island on 30 March 1999, and we did the same for females on 2 April 1999; we then compared the distribution of plumage coloration in these groups with that of birds that were feeding 1-year-old offspring in 1999.

Breeding Population Size and Spatial Genetic Structure

In 1998 and 1999, we conducted daily counts of the frigatebird colony by following a regular survey route that took us within 50 m of all individuals on the Island (see Dearborn et al., 2001a). During these surveys, we counted individuals in three age classes (1 – 2 year old juveniles, 3 – 6 year old subadults, and adults), two sex classes (for adults only), and three location classes (perched, on nest, and flying). The number of birds on nests at any given time is only a minimum count of the number of nesting attempts and number of birds attempting to nest that year, because the majority of nests fail. To better estimate the number of nesting attempts and the number of adults participating in these attempts, we combined estimates of fledging success at those nests that were monitored during the 1999 season, the number of chicks fledged across the entire colony that season (as revealed in a census made in August), and the frequency of nesting attempts by marked males and females. We calculated the total number of nesting adults in the colony as (# fledged)/(estimate of reproductive success)x(mean # nest attempts for marked males and females). Last, we combined this calculation with our measurement of pairing success for males and females, to yield an estimate of the total number of individuals that attempted to attract a mate (in the case of males) or choose a mate (in the case of females) in that breeding season.

Our previous research on this population had suggested an absence of strong spatial genetic structure to the breeding colony, as assessed with multilocus minisatellite fingerprinting (Cohen and Dearborn, 2004). Here, we use a separate data set to assess the robustness of this finding. In an analysis of population genetic structure among Tern Island, Johnston Atoll, and Christmas Island (Kiribati), we analyzed AFLP data from 117 polymorphic loci (Dearborn et al., 2003), finding significant differentiation among the three islands. Here, we use Spatial Genetic Software v. 1.0c (SGS; Degen et al., 2001) to test for spatial autocorrelation among the Tern Island samples. For each bird that was sampled, we mapped its breeding location on a coordinate grid of the Island and then used SGS to generate eight sets of pairwise combinations of birds whose nests fell into a particular category based on physical distance between the two nests. In this manner, we made sets of all pairs of birds whose nests were within 50 m of each other, within 50-100 m of each other, within 100-150 m of each other, and so forth up to a 350-400m category. Within each distance category, SGS computes the mean of the genetic dissimilarity between each possible pair of sampled birds, using Tanimoto distance for dominant markers such as AFLPs. Plotting the mean genetic dissimilarity ordered across the eight distance categories tests whether there is spatial genetic structure to the population. A 1000-run Monte Carlo permutation test was used to generate confidence intervals for this relationship.

RESULTS

Pairing Success of Males and Females

Of the 76 tagged males that were in breeding plumage, 64 (84.2%) attempted to attract a mate at some point during the 2000 breeding season, but only 12 (18.75%) succeeded in pairing. Four of the 12 had a nest with a female but no egg, and an egg was laid at the remaining eight nests. None of the marked males nested twice within that breeding season.

Of the 51 tagged females that were in breeding plumage, 28 (54.9%) evaluated the pool of displaying males at some point during the breeding season, and 25 (89.3%) nested (5 of the 25 had a nest with a male but no egg, and 20 laid an egg). Of the 25 females that nested, 8 nested more than once in the season (following nest failure), including 1 that laid an egg on three different breeding attempts within one season.

Individual males were thus much more likely to try to mate than were females (84.2% vs. 54.9%; $X^2 = 13.132$, df = 1, p = 0.0003), but the males that tried to attract a mate were only one-fourth as likely to succeed as females (18.75% vs. 89.3%; $X^2 = 40.307$, df = 1, p < 0.000001). Among those birds that did nest, females were more likely to nest again after nest failure than were males (Fisher exact p = 0.036). For those birds that tried to acquire a mate, there was more within-sex variation in pairing success for males than for females (for number of nesting attempts: male CV = 2.098, female CV = 0.601, and 95% confidence intervals do not overlap).

Reproductive Success

Hatching success was 24.7% (45 of 182 nests) in 1998, 28.4% (74 of 261 nests) in 1999, and 23.5% (4 of 17 nests) in 2000. Using those nests with definitively known lay dates, there was no seasonal change in hatching success in 1998 (logistic regression, n = 118 nests from 25 February to 4 June 1998: Wald X^2 = 0.889, df = 1, p = 0.346). In 1999, there was also no significant seasonal change in hatching success (logistic regression, n = 231 nests from 7 February to 30 May 1999: Wald X^2 = 2.672, df = 1, p = 0.102). Fledging success was 63.5% (47 of 74 nestlings that hatched) in 1999; thus, overall reproductive success was 18.0% (47 fledglings from 261 nests).

Duration of Breeding Cycle and Breeding Frequency Across Years by Males and Females

We recorded 373 feeding events to 1-year-olds in 1998 and 374 feedings to 1-year-olds in 1999. In January and February, during the early part of the breeding season, roughly one-third to one-half of feedings to 1-year-olds was made by males (Fig. 1). As the new breeding season progressed, however, male effort tapered off, such that nearly all feedings observed in April, May, and June were made by females. This clearly indicates a difference in the duration of parental effort by males and females, though it does not address whether their care for a 1-year-old nestling prohibits them from attempting to start a new nest that same season.
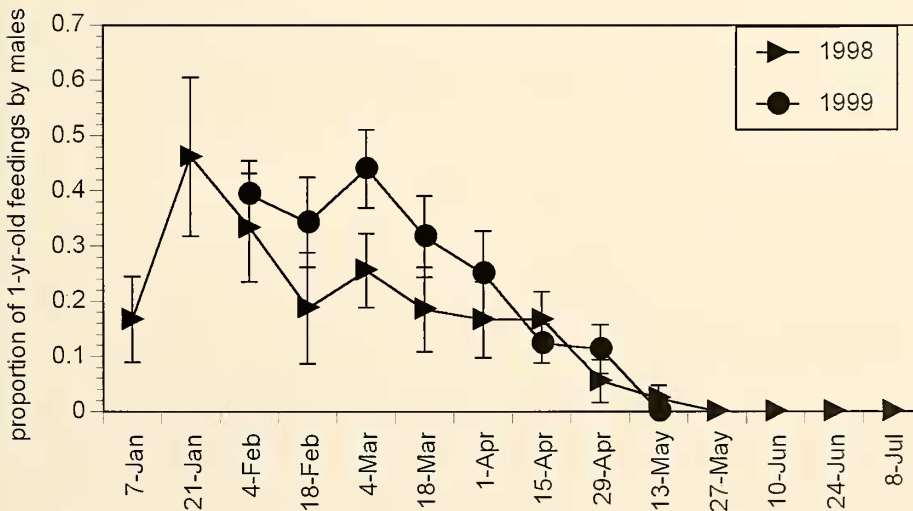

Figure 1. Feedings to 1-year-old great frigatebird fledglings made by males and females on Tern Island in 1998 and 1999. Total sample size was 373 and 374 feeding observations in 1998 and 1999, respectively.

Male plumage varied primarily in breast coloration, ranging from black to gray to brown. Based on five categories of breast coloration, we found that the males feeding 1-year-old offspring in 1999 were more likely to be brown than were males on new nests or males trying to attract a mate in that year, and males trying to attract a mate were more likely to have substantial amounts of white in the breast plumage than males who
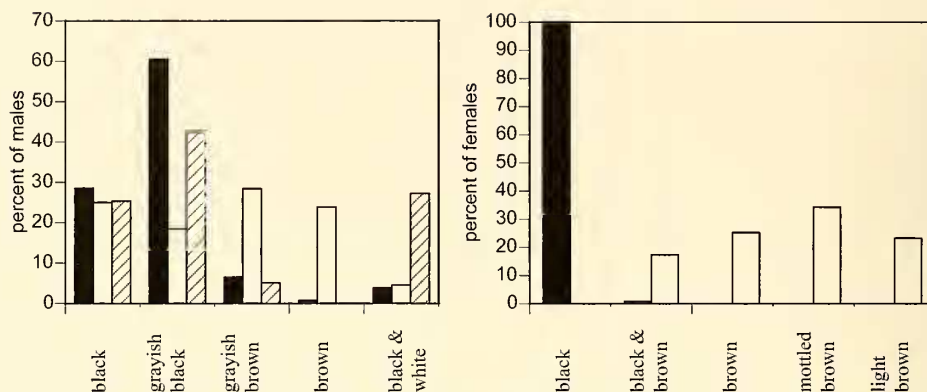
Figure 2. Plumage of great frigatebirds feeding 1-year-old fledglings and birds engaged in new breeding attempts on Tern Island in 1999. a) Breast plumage categories of males that were feeding 1-year-olds (open bars) or displaying to attract a mate (hatched bars) or tending a new egg or chick (solid bars). b) Head plumage categories of females that were feeding 1-year-olds (open bars) or tending a new egg or chick (solid bars).

had already been chosen as mates that season ($X^2 = 222.837$, df = 8, p << 0.00001; Fig. 2). This whiter breast plumage is likely indicative of males that are just reaching sexual maturity (Metz and Schreiber, 2002).

Female plumage varied primarily in head coloration, ranging from black to light brown. Based on categories of head coloration, we found that females feeding 1-year-old offspring in 1999 were almost exclusively black-headed, whereas no females on new nests that year were black-headed ($X^2 = 488.343$, df = 4, p << 0.00001; Fig. 2).

Breeding Population Size and Spatial Genetic Structure

Daily counts in 1998 and 1999 revealed as many as 1,171 males, 1,053 females, and 691 juveniles and subadults on the Island at a single time (Fig. 3). In both years, the number of juveniles and subadults was fairly constant over time. In contrast, the total number of adults on the Island fluctuated greatly and generally increased all the way through the pair-formation and egg-laying portion of the breeding season, even though the rate of pairing declined dramatically in May and June. By July, most nests had failed or had reached ages when chicks are unattended except when being fed, and most of the adults on the Island were not engaged in reproductive activity. We previously (Dearborn et al., 2001a) described a seasonal shift in the ratio of males to females that are unpaired and potentially available for mating. This ratio becomes less biased because of a gradual increase in the number of females on the Island (Fig. 3). Here, we apply the plumage criteria described in the previous section to assess whether these females are likely breeders. Plumage-specific daily counts of females were conducted in 1999 only. From January through March of 1999, most of the females on the Island had black head plumage, indicative of current breeders; females with brown or mottled heads were rare, perhaps because they were on the Island only while feeding 1-year-olds. As the number
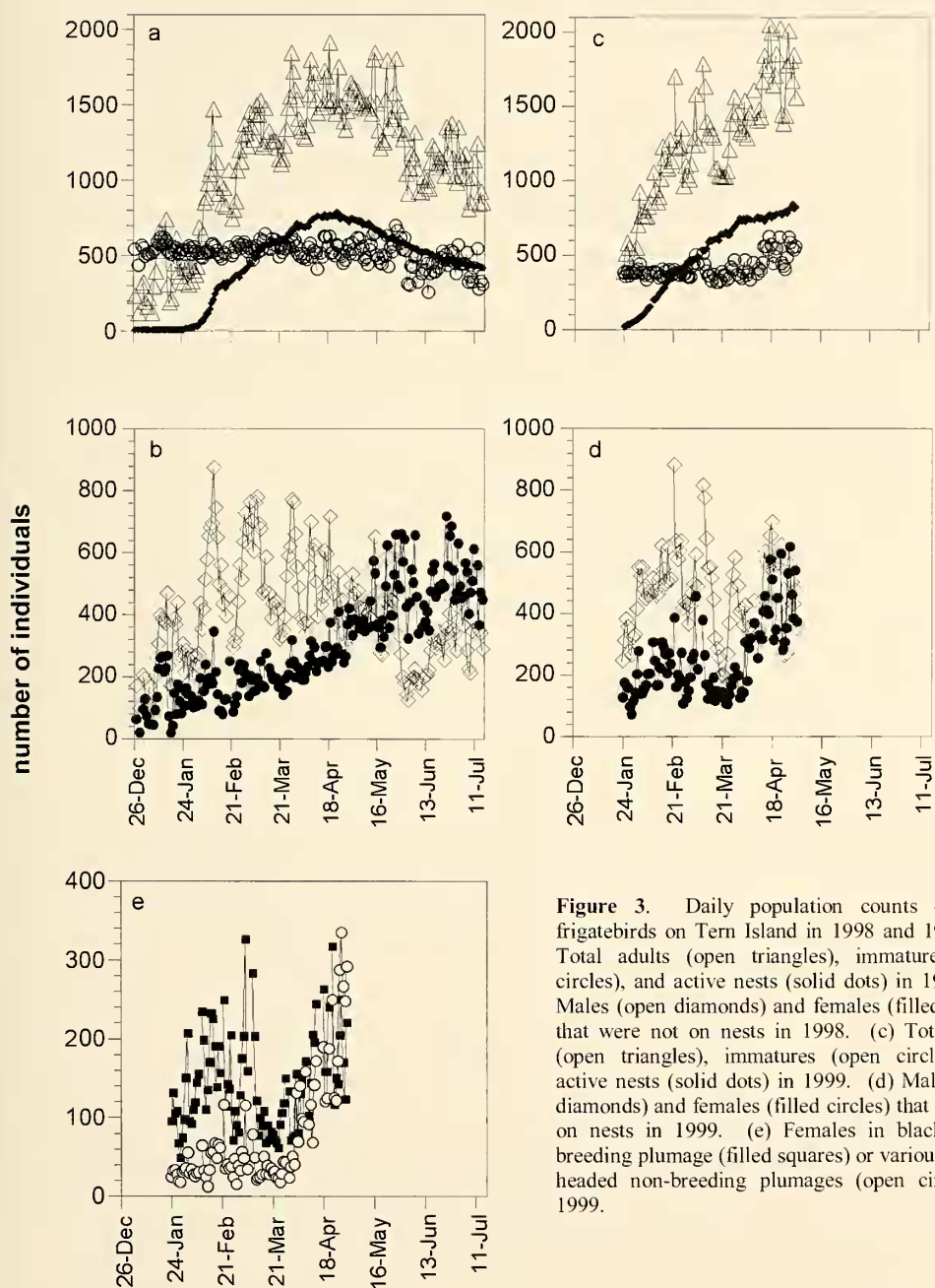
Figure 3. Daily population counts of great frigatebirds on Tern Island in 1998 and 1999. (a) Total adults (open triangles), immatures (open circles), and active nests (solid dots) in 1998. (b) Males (open diamonds) and females (filled circles) that were not on nests in 1998. (c) Total adults (open triangles), immatures (open circles), and active nests (solid dots) in 1999. (d) Males (open diamonds) and females (filled circles) that were not on nests in 1999. (e) Females in black-headed breeding plumage (filled squares) or various brown-headed non-breeding plumages (open circles) in 1999.

of females on the Island increased in April, a decreasing proportion of females were black-headed, meaning that most of the "new" females on the Island were non-breeders (Fig. 3e).

In an Island-wide census in late August 1999 (USFWS, unpublished data), we found 378 nestlings. Because there was no mortality at individually marked nests between late July and the fledging of the last chick in December, and because no nestlings at marked nests fledged before late September, it can be assumed that 378 is a good estimate of the number of frigatebird nestlings that fledged on Tern Island in 1999. Applying our estimate of reproductive success at marked nests during that year (18.0%), there were approximately 2,099 nests initiated during the 1999 breeding season. Among those birds that were marked at the start of the 2000 season (the only year for which we have such data from early-marked females) and then initiated nests (i.e., laid an egg) that year, the mean number of nests initiated per female was 1.30; for males, the mean number of nest attempts was 1.00. If these numbers are relatively constant across years, the population of frigatebirds actually nesting on Tern Island in 1999 likely consisted of approximately 1,615 females (2,099 nests with eggs / 1.30 eggs per female) and 2,099 males. This estimate can be combined with our measure of pairing success for females (89.3%) and males (18.75%) to estimate the number of adults that attempted to breed (i.e., including those that did and did not reach the stage of nest building). By this approach, the pool of birds attempting to breed in 1999 consisted of approximately 1,809 females (1,615 / 0.893) and 11,195 males (2,099 / 0.1875). Including those adults not breeding in 1999 (whether at sea, on other islands, or on Tern Island but not currently breeding), the total number of sexually mature adults in the Tern Island population is likely even larger, given that plumage evidence (see above) suggests that individuals whose nests succeed are likely to skip breeding for at least the following year.

Spatial analysis of AFLP data revealed no significant change in pairwise genetic dissimilarity between breeders across the categories of distance between nest sites, as the confidence interval for the Tanimoto dissimilarity index within each distance category spanned the overall mean of 0.3447. Thus, AFLP data suggest no spatial genetic structure within the Tern Island breeding colony, consistent with the finding of very little structure based on the multilocus minisatellite fingerprinting data (Cohen and Dearborn, 2004).

DISCUSSION

This study sheds light on basic demographic processes in this population. We found that in a given year males were much more likely than females to try to obtain a mate but were much less likely to succeed at pairing. This difference in pairing success between the two sexes is consistent with behavioral descriptions of mate acquisition (which seems to consist entirely of female choice; Nelson, 1975) and with a male-biased operational sex ratio (Dearborn et al., 2001a). Females, but not males, occasionally nest multiple times in a season if the first nest fails; this difference between sexes is due to the difficulty that males have in attracting a mate, rather than to lack of interest in re-nesting by males. Overall, the coefficient of variation in pairing success was much greater for

males than females; this provides evidence that sexual selection is stronger on males in this population and supports the notion that the male-biased operational sex ratio is linked to sexual selection via variation in pairing success.

Following pair formation and egg laying, nesting attempts had a very low probability of success. Although fledging success was high, hatching success was below 30% in all three years of this study. Frigatebird reproductive output is affected by El Niño conditions at colonies further south in the Pacific (Schreiber and Schreiber, 1989), but our three years with low success included an El Niño year (1998), a La Niña year (1999), and a year of moderate Southern Oscillation Index. Overall reproductive success was towards the low end of the range reported from other populations (Metz and Schreiber, 2002), though hatching success on Tern Island was somewhat higher in 2003 than in previous years (Juola and Dearborn, in press). Nests failed during incubation for a variety of reasons, but three main causes seem to be aggressive interactions with other frigatebirds, severe weather events, and prolonged foraging trips by the mate that is currently off the nest (Dearborn, 2001). Aggressive interactions could reduce nest success of frigatebirds in a density-dependent manner (Reville, 1988; 1991), though we do not yet have such data for Tern Island. Prolonged foraging trips by a breeding bird are important because the body condition of the frigatebird currently incubating becomes a limiting factor in its ability to stay on the nest and continue fasting (Dearborn, 2001). This, coupled with analyses of other seabird populations on Tern Island (Dearborn et al., 2001b), suggests that resource availability is a key component of individual- and population-level reproductive success for these birds.

Plumage data indicate that females do not breed in years following a successful breeding attempt; the plumage of those females feeding 1-year-old offspring was categorically different from that of females incubating eggs or new nestlings. For males, the findings are more complex. Males feeding 1-year-olds were much more likely to have brown breast plumage than males with eggs or new nestlings, but there was substantial overlap between the two groups of males. Either plumage is a less discriminatory indicator of breeding status in males than in females or some males are simultaneously feeding 1-year-olds and tending new nests. For both sexes, feather wear in the absence of molt is the likely mechanism by which birds feeding 1-year-olds are browner than birds involved in new breeding attempts, as brown is the basal coloration of black-tipped head and breast feathers in great frigatebirds (Metz and Schreiber, 2002). Overall, these observations are consistent with the long-standing hypothesis that male frigatebirds try to breed annually and females biennially (Stonehouse and Stonehouse, 1963; Diamond, 1973; Nelson, 1975; Trivelpiece and Ferraris, 1987; Carmona et al., 1995), but the evidence presented here is indirect. Note also that this hypothesis of unequal breeding frequencies of males and females was driven by observations of magnificent frigatebirds (*Fregata magnificens*), in which males abandon the care of nestlings after just a few months (Osorno, 1999). We have shown in this study that males in our population do taper off their parental care of fledglings sooner than do females, but male care extends well into the pair-formation part of the next breeding season.

Colony-wide counts detected as many as 1,171 males, 1,053 females, and 691 juveniles on the Island at a single time. However, the frequent turnover of birds,

revealed by mark-resight data, indicates that the true number of adults using the Island is many times larger than this. Individuals vary extensively in their pattern of Island use (unpublished data), such that some individuals visit only briefly, others stay for weeks, and yet others come and go regularly over the course of many months. Similar complexities were seen in patterns of visits to other islands (e.g. Johnston Atoll) by frigatebirds that were wing-tagged on Tern Island (Dearborn et al., 2003). In light of these complexities in space use, the best way to define a population may be based on breeding individuals. Using a combination of nest counts and reproductive metrics, we estimated that 1,615 females and 2,099 males nested on Tern Island in 1999; this relatively small difference in number of breeders of the two sexes reduces the effective population size only slightly (from 3,714 to 3,651 in a given year; Kimura and Crow, 1963). Many additional birds attempted to breed but did not progress beyond the pair-formation stage. Based on the pairing success of marked individuals, we estimated that the pool of birds attempting to breed on Tern Island in 1999 was larger, particularly for males: 1,809 females and 11,195 males. Because plumage evidence suggests that birds are unlikely to breed in successive years, at least in years following the fledging of a chick, the actual size of the breeding population may be even larger. Our estimate of the number of birds breeding on Tern Island is substantially higher than the previous estimate for this population (300 – 375 pairs; Metz and Schreiber, 2002), and may reflect more exact information or an increasing population, or both; population increase in French Frigate Shoals is suggested by nest counts over the past 40 years (summarized in Cohen and Dearborn, 2004). Given that the global population of great frigatebirds has been estimated as only 54,000 – 68,000 breeding pairs (Metz and Schreiber, 2002), the Tern Island population may be a demographically significant one.

Using AFLP genetic markers, we found no evidence of spatial genetic structure within the Tern Island colony. This is consistent with our understanding of the history of this population and with our previous findings with multilocus minisatellite fingerprinting (Cohen and Dearborn, 2004). The lack of small-scale spatial structure alleviates the need to account for this in localized management decisions, although our earlier finding of substantial genetic differentiation among Tern Island, Johnston Atoll, and Christmas Island (Dearborn et al., 2003) is important.

A crucial gap in our knowledge of frigatebird ecology in the Northwestern Hawaiian Islands is foraging movements and destinations, particularly given the connection between reproductive success and adult body condition (Dearborn, 2001). Diet samples of frigatebirds in Hawaii show a preponderance of flying fish (Exocoetidae) and squid (Ommastrephidae; Harrison et al., 1983), but not knowing where the birds are foraging makes it difficult to assess potential threats to food availability. One plausible threat is the commercial fishery for large predatory fish, because a reduction in the number of such fish could reduce the frequency with which frigatebirds' prey are driven to the surface (Safina and Burger, 1985). Stocks of large piscivorous fish have declined markedly, both globally (Myers and Worm, 2003) and in the central Pacific (Cox et al., 2002). The ecological interaction between predatory fish and frigatebirds is a critical one because frigatebirds neither dive nor swim after their own prey. Furthermore, because frigatebirds soar in thermals extensively when traveling (Wcimerskirch et al., 2003), they

may spend little time close enough to the surface to readily detect patchily distributed prey, which could heighten their dependence on the activity of predatory fishes. Mark-resight data (Dearborn et al., 2003) have reinforced the hypothesis that these birds routinely travel widely, but satellite telemetry studies such as those now being conducted in Madagascar (Weimerskirch et al., 2004) are needed to better delineate the flight patterns and foraging habitats of Hawaiian frigatebirds.

Overall, great frigatebirds are thought to be experiencing population declines, though this trend is geographically variable (Metz and Schreiber, 2002). Threats to frigatebirds in other parts of their range include habitat loss, nest site destruction by exotic herbivores, nest predation by exotic mammals, and human disturbance or predation (summarized in Metz and Schreiber, 2002), factors that are not currently threats in the Northwestern Hawaiian Islands. Frigatebirds are long-lived, they are slow to mature, and they are very limited in their reproductive output. Consequently, population declines resulting from increased adult mortality or decreased productivity would take many years to recover, such that we need to guard against them carefully. Because of the large and relatively well-protected populations of great frigatebirds and other seabird species in the Northwestern Hawaiian Islands, continued protection of these islands is crucial for seabird conservation.

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